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REVIEW

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Multifaceted mechanisms and roles of phosphate-solubilizing microorganisms in enhancing phosphorus availability for sustainable agriculture

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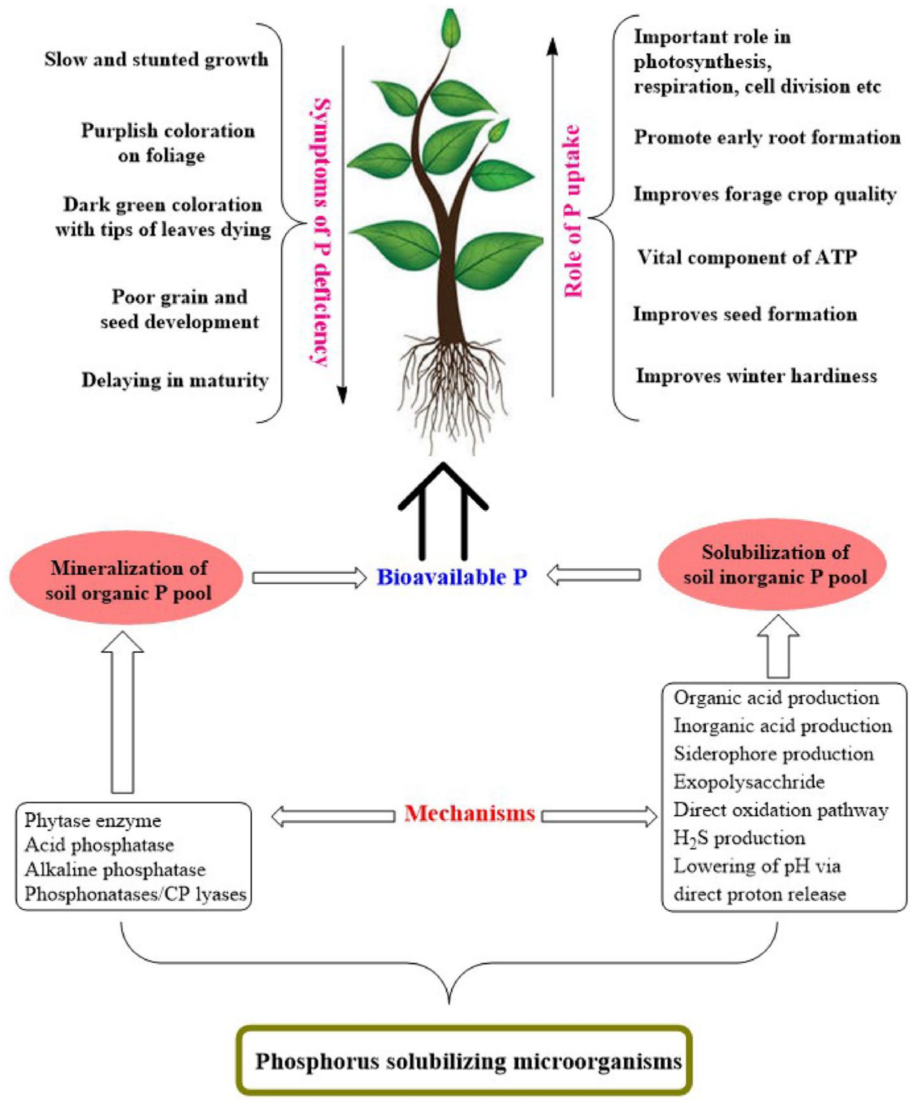
Abstract
Phosphorus is an essential macronutrient for plant growth, yet its availability in soils is often limited due to its predominance in insoluble forms, with less than 1% accessible for plant uptake. This review explores the role of phosphate-solubilizing microorganisms (PSMs) in enhancing phosphorus availability, especially in phosphate-deficient soils of cereals, pulses and horticulture crops in agricultural systems. PSMs include specific strain of bacteria and fungi that facilitates the transformation of insoluble phosphorus into forms that are readily absorbable by plants, thereby improving crops and promoting sustainable agricultural production. Different mechanisms employed by PSMs, such as the secretion of organic acids, which lower soil pH, and enzymes that aid in mineralization processes, function of genes involved during solubilization, thereby increasing their bioavailability and their interactions with plant roots that enhance nutrient uptake by contributing to biological nitrogen fixation and overall soil health and fertility. Furthermore, it addresses the global challenge of phosphorus deficiency and emphasizes the necessity for effective management strategies that incorporate PSMs to ensure food security amid rising agricultural demands. PSMs represent a promising strategy for future agricultural resilience, as more than 40% of the world's cultivated land suffers from insufficient phosphorus utilization of PSMs offer a sustainable alternative to chemical fertilizer, which leads to environmental degradation through runoff and soil erosion.

Keywords Phosphorus solubilizing microorganisms, Phosphorus availability, Sustainable agriculture, Soil health, Soil fertility and fertilizers

1 Introduction

Phosphorus is a crucial macronutrient for plants, playing a key role in energy transfer, photosynthesis, and the synthesis of nucleic acids, mainly as a part of ATP. However, it is plentiful in the lithosphere but frequently not accessible to plants because it exists in insoluble forms, with less than 1% of the total soil phosphorus being available for uptake.

Graphical abstract



This availability is influenced by optimal soil pH levels, which range from 6.0 to 7.0 [104]. Organic phosphorus makes up 10–50% of the total phosphorus in different soils and needs to be mineralized by soil microorganisms into inorganic forms before plants can absorb it [80]. Generally, only about 15–25% of the phosphorus fertilizers applied are taken up by crops, while the remainder is either fixed in the soil or lost through leaching [65].

The global average concentration of inorganic labile phosphorus is estimated to be 187 kg P/ha for cropland and 91 kg P/ha for grassland. Rock phosphate-derived fertilizers are widely used in agriculture as a source of inorganic phosphorus (P_i), which is more readily available for crops in the form of orthophosphate. However, P_i can become bound to soil clay particles and precipitate with divalent cations or be transformed into organic forms, which diminishes its availability to plants [35, 110]. Excessive application of phosphorus can lead to environmental issues such as soil erosion, leaching and runoff [17, 97].

Phosphorus availability is greatly influenced by the type and composition of the soil; sandy soil exhibits higher leaching rates and poorer retention than clay [33]. In acidic soils, phosphorus binds with iron and aluminium phosphates, but in alkaline soils, calcium phosphate limits its availability [2, 63]. By converting insoluble phosphorus into forms that plants can easily absorb, phosphate-solubilizing microorganisms (PSMs) significantly increase soil fertility and, consequently, agricultural yields [128]. Research on plant growth-promoting bacteria (PGPB), particularly in regard to their interactions with plant roots, has significantly increased since 2000 [138, 141, 143]. Through activities including solubilization, mobilization and mineralization, both bacteria and fungi contribute to the phosphorus cycle in agricultural soil that is deficient in phosphorus. These processes also have an impact on the dynamics of sorption–desorption and dissolution precipitation [114]. The microbial community in this region is greatly influenced by the growth of roots and the accumulation of organic matter in the rhizosphere [57, 114]. In phosphorus-deficient soils, bacteria and fungi inoculation can further modulate the expression of phosphorus transporter genes in roots by stimulating phytohormone production and enhancing P-hydrolysing enzyme activity, thereby improving root structure and phosphorus uptake efficiency [14, 123]. Beyond the role in enhancing phosphorus availability, PSMs also directly influence plant growth through root-related mechanisms [88]. Some bacterial strains synthesize phytohormones such as indole-3-acetic acid (IAA), which modify root system architecture in crops, including wheat and maize [45, 123]. A recent study by Elhaissoufi et al. [41] underscored the significance of plant-root interactions under low-phosphorus conditions, revealing strong associations between root physiological and morphological traits and efficiency of phosphorus utilization in aboveground biomass. By highlighting the various ways in which PSMs increase phosphorus bioavailability and their useful uses in boosting soil fertility, we aim to summarize recent developments in our knowledge of PSMs. This review emphasizes the potential of PSMs as an environmentally acceptable substitute for chemical fertilizers and promotes their broader use to address upcoming issues with food security and agricultural resilience in a changing global environment.

2 Deficiency of phosphorus in agricultural soil

More than 40% of the world's cultivated land lacks enough phosphorus, which is necessary for plant development, making phosphorus deficit in agricultural soil a serious problem [121]. By 2050, there will likely be 10 billion people on the planet, which would significantly boost food demand while agricultural output rises by 80 to 90%. The yields of vital crops like wheat, rice and maize, however, may be in jeopardy due to phosphorus deficiency [89]. There is a severe phosphorus shortage in parts of Africa, South America and Eastern Europe. One significant contributing element is soil erosion, which results in annual phosphorus losses of 4–19 kg per hectare, or more than 50% of the overall phosphorus losses [5].

Topsoil, which is rich in nutrients, including phosphorus, is lost as a result of soil erosion, particularly from water runoff. Overuse of chemical fertilizers can cause nutritional imbalances, which, over time, can lower the soil's phosphorus levels even further [5]. The availability of phosphorus in soil depends on the different environmental factors such as soil type, soil pH, organic matter content, erosion and microbial activity (Table 1). By adversely affecting soil health and nutrient cycling, poor soil management

Table 1 Different factors influence phosphorus availability in soil

Factor	Description	Impact on phosphorus availability	Management strategies	References
Soil type	Sandy vs. clay	Sandy soils have higher leaching rates, reducing phosphorus retention	Use of organic amendments	Sharma et al. [115], Johan et al. [63]
Soil pH	Acidic vs. alkaline conditions	Affects the solubility of phosphorus	pH adjustment through lime or sulfur	Bindraban et al. [17], McDowell et al. [89]
Organic matter content	Presence of decomposed plant material	Enhances nutrient cycling and availability	Regular incorporation of organic matter	Peñuelas et al. [97], Cordell et al. [30]
Erosion	Loss of topsoil due to water runoff	Significant phosphorus loss from agricultural soils	Soil conservation practices, contour farming	Alewell et al. [5], Rosen [106]
Microbial Activity	Presence and diversity of soil microorganisms	Enhanced phosphorus solubilization and cycling	Inoculation with PSM, crop rotation	Khan et al. [64], Debicka et al. [33]

techniques such as insufficient crop rotation and a lack of organic matter exacerbate this shortage [106].

A lack of phosphorus can reduce agricultural yields, stunt plant development and degrade the nutritional value of food. For instance, a lack of phosphorus can have a detrimental effect on flowering and seed formation, which lowers grain protein content and lowers crop quality overall [29, 30]. In addition, land use changes and intensive agricultural practices can disturb natural phosphorus cycling and restrict the pool of plant-available phosphorus in many agroecosystems, as well as soil degradation [61]. It reduces the availability of essential minerals in our food supply,this deficit has broader effects on human health and nutrition in addition to impeding agricultural output.

To alleviate phosphorus deficit, a number of management strategies have been put into place, including the use of chemical fertilizers, organic amendments and improved crop management methods. Crop rotation, intercropping and the use of cover crops are among strategies that have been shown to increase soil phosphorus availability and improve soil health in general [119]. These management techniques do, however, come with several difficulties. Many farmers' access to chemical fertilizers is restricted by their high cost, particularly in developing nations. Moreover, eutrophication, in which an excess of phosphorus discharge causes algal blooms and the deterioration of aquatic ecosystems, can be brought on by an over-reliance on chemical fertilizers. Adoption of more efficient phosphorus management techniques may also be hampered by farmers' ignorance of and lack of education on sustainable soil management techniques. Applying effective microbial strains may be a more successful tactic for reducing soil phosphorus deficiency [72].

3 Phosphate-solubilizing microorganisms

The phosphorus cycle depends on a variety of PSMs, which convert insoluble phosphorus compounds into plant-available forms, enhancing crop productivity and promoting sustainable agriculture. These include fungi (e.g. *Aspergillus*, *Penicillium*, *Mucor*, and Arbuscular Mycorrhiza), Actinobacteria and Cyanobacteria (*Anabaena* and *Westiellopsis*), as well as bacteria (*Bacillus*, *Pseudomonas*, and *Rhizobium*). In addition to these, yeasts like *Candida krusei*, *Torulaspora globosa*, *Rhodotorula*, *Debaryomyces hansenii*, *Saccharomyces cerevisiae* and *Aureobasidium pullulans* have demonstrated effective phosphate solubilization through mechanisms such as organic acid production, phosphatase activity and chelation [4, 31]. The diversity and abundance of PSMs are influenced by the soil type, land use and environmental conditions, with population present in both rhizospheric and non-rhizospheric soil. Generally, phosphate solubilizing fungi constitute about 0.1–0.5% of the total soil fungal community, while phosphate-solubilizing bacteria account for 1–50% of the bacterial community [56]. Their populations are often greater in phosphorus-deficient soil, reflecting adaptive strategies for nutrient mobilization and their distribution is closely linked to soil phosphorus status across different agroecosystems. Management practices strongly influence PSM abundance and diversity. The diversity and solubilization efficiency of PSMs, where mostly rock phosphate was used as the complex form of phosphate, are summarized in Table 2. Khan et al. [64] reported that organic farming systems, particularly in the crop rhizosphere, support higher PSM population, whereas heavy reliance on synthetic fertilizers can suppress the establishment of beneficial microbes. Complementary findings by Wani et al. [133] showed that integrating organic and inorganic inputs fosters greater microbial diversity than chemical fertilizers. In semi-arid regions such as Eastern Kenya, where resource-poor smallholder farmers face limited access to costly fertilizers, Janati et al. [62] demonstrated that indigenous PSM diversity plays a pivotal role in sustaining soil fertility. Their survey identified 71 Phosphate Solubilizing Bacteria (PSB) isolates spanning 23 morphotypes and genera, including *Burkholderia*, *Pseudomonas*, *Bacillus* and

Table 2 List of potential phosphate-solubilizing microorganisms

Microbial group	Phosphate solubilizers	Solubilization results (mg/L)	References
Bacteria	*Bacillus megaterium*	394.2	[32]
	Bacillus subtilis	210.4	[32]
	Bacillus pumilus; Bacillus coagulans	195.42; 130	[10, 59]
	Bacillus circulans	130	[59]
	Bacillus thuringiensis	24.21	[16]
	Thiobacillus ferrooidans	45	[24]
	Pseudomonas putida	305.5	[126]
	Pseudomonas fluorescens	618.57	[53]
	Pseudomonas striata	56.11	[53]
	Rhizobium meliloti	120	[28]
	Rhizobium leguminosarum	197.1	[130]
	Acinetobacter rhizosphaerae	291–454	[9]
	Streptomyces cyaneus	70.36	[71]
Fungi	*Aspergillus niger*	1.52	[39]
	Aspergillus clavatus	1.135	[38]
	Aspergillus awamori	250	[71]
	Penicillium citrinum	514.44	[43]
	Penicillium lilacinium	175	[114]
	Penicillium funicolosum	520	[126]
	Penicillium rubrum; Penicillium simplicissiumum	200	[112]
	Arthrobotrys oligospora	320	[53]
	Trichoderma viride	61.96	[112]
Cyanobacteria	*Calothrix braunii*	283.16	[114]
Yeast	*Saccharomyces cerevisiae*	41.2; 52	[31, 142]
	Torulaspora globosa	38.4	[4]
	Candida krusei	45.3	[31]
	Debaryomyces hansenii	22.9	[95]
	Rhodotorula	32.1	[92]

Enterobacter, with abundance inversely related to soil nutrient levels-particularly, particularly calcium, phosphorus and iron, indicating adaptive dominance under nutrient-depleted conditions [3, 88].

4 Mechanism of phosphate solubilization by phosphate solubilizing microorganisms

The production of complex or mineral-dissolving substances, including organic acid anions, siderophores, protons, hydroxyl ions and CO_2, is one of the ways that microorganisms solubilize phosphorus (P) (Table 3; Fig. 1). Furthermore, they create extracellular enzymes that facilitate biological P mineralization, a process known as the biochemical mineralization of phosphorus and the release of P after substrate destruction [90]. Thomas and Pierzynski [127] also highlighted three main processes that influence soil solution P concentrations: (1) dissolution–precipitation (mineral equilibria), (2) sorption–desorption (interactions between P in solution and soil solid surfaces) and (3) mineralization–immobilization (biologically mediated conversions of P between inorganic and organic forms).

4.1 Inorganic phosphate solubilization

The following processes result in the solubility of inorganic phosphates in soil, such as Fe–P, Al–P, and Ca–P.

4.1.1 Production of organic acids

One predominant mechanism involves secretion of organic acids (e.g., gluconic, citric, oxalic, malic, tartaric, and lactic acids) that chelate cations bound to phosphate, lower the pH and disrupt metal–phosphate complexes [67, 68]. Organic acid production can occur via microbial fermentation, respiration of organic carbon compounds, or direct oxidation of glucose.

Table 3 Mechanisms of phosphate-solubilizing microorganisms

Microorganism type	Examples	Mechanism of phosphate solubilization	Optimal conditions for growth	References
Phosphate Solubilizing Bacteria (PSB)	*Bacillus megaterium*, *Pseudomonas fluorescens*, *Bacillus subtilis*	Production of organic acids and enzymes that solubilize phosphate	Neutral to slightly alkaline pH, warm temperature	Khan et al. [65], Tian et al. [128]
	Streptomyces albus, *Nocardia*	Decomposition of organic matter enhances phosphorus availability	Well-drained soil, moderate temperatures	Bünemann et al. [22], Clausing and Polle [27]
Phosphate Solubilizing Fungi	*Aspergillus niger*, *Penicillium*, *citrinum*, *Mucor*	Production of organic acids (e.g., Citric acid), lower pH and enhanced solubilization of phosphates from insoluble sources like tricalcium phosphate	Moist conditions, varying pH levels	Debicka et al. [33], Sawers et al. [109]
	Rhizophagus irregularis, *Glomus*	Enhancement of root surface area for nutrient exchange, facilitating the uptake of phosphorus from soil and increasing its availability through symbiotic relationships with plants	Diverse soil types, symbiotic relationship with host plants	Liu et al. [82], Elhaissoufi et al. [41]
Cyanobacteria	*Anabaena*, *Westiellopsis*	Solubilization of phosphorus from rock phosphate primarily occurs through the secretion of organic acids and the formation of chelates that mobilize phosphorus	Alkaline conditions, presence of light	Adnan et al. [3], Manzoor et al. [88]

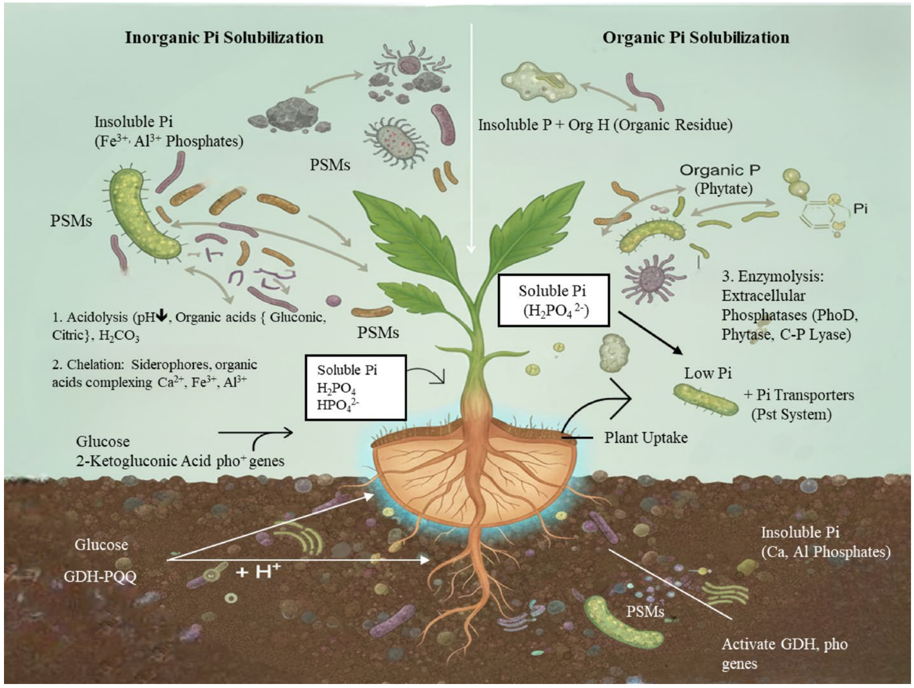


Fig. 1 Schematic representation of microbial phosphorus solubilization mechanisms in the rhizosphere. PSMs enhance soil P availability by converting insoluble inorganic and organic phosphates into plant-available orthophosphates through organic acid secretion, proton extrusion and enzymatic mineralization. Note: PSMs = Phosphate-solubilizing microorganisms; Pi = inorganic phosphate (typically present as orthophosphate anions); GDH = Glucose dehydrogenase; PQQ = Pyrroloquinoline quinone; pho genes = part of phosphate (Pho) regulon, a global regulatory system in bacteria induced in response to phosphate starvation; Pst system = Phosphate-specific transport system, a high-affinity ATP-binding cassette transporter responsible for the uptake of Pi under low phosphate conditions

The gluconic acid pathway, widely reported among *Pseudomonas*, *Bacillus* and *Rahnella* species, is mediated by glucose dehydrogenase (GCD) in the bacterial periplasm. The gcd gene encodes this quinoprotein enzyme, while its redox-active cofactor, pyrroloquinoline quinone (PQQ), is synthesized by the pqqABCDEF gene cluster [131]. Disruption of pqqA in *Rahnella aquatilis* HX2 reduced gluconic acid concentration from 9.68 to 0.65 g L^{-1}, accompanied by a drop in soluble P from 465.9 to 99.7 mg L^{-1} [78].

Certain *Pseudomonas* sp. (strain AZ15) produces oxalic, gluconic, acetic, lactic and citric acids, enabling P solubilization up to 109.4 mg L^{-1} while improving chickpea nodulation, biomass, yield, and nodule number [137]. In soybeans, *Trichoderma* strains AMS34.39, AMS31.15, and AMS1.43 solubilize P primarily through acids like ascorbic, citric, malic, gluconic and phytic acid. Collectively, acidification via organic acids remains the most widely documented method for inorganic P solubilization [49].

4.1.2 Inorganic acid and H_2S production

In addition to organic acids, microorganisms can produce inorganic acids (e.g., HCl, HNO_3, H_2SO_4, H_2CO_3), which also contribute to phosphate solubilization, albeit less effectively [85, 116]. Certain *Nitrobacter* and *Thiobacillus* spp. solubilize P via nitric and sulfuric acid production. Sulfur-oxidizing bacteria like *Delftia* sp. SR4 convert thiosulfate and elemental sulfur to sulfate, increasing P availability [47].

Hydrogen sulfide (H_2S), a by-product of sulfate reduction and organic matter decomposition, can also facilitate P release [87]. *Brassica juncea* inoculated with efficient PSM strains demonstrated 116% higher P-solubilizing efficiency compared to uninoculated controls [107].

4.1.3 Proton release from NH_4^+ (Assimilation/Respiration)

Microbial assimilation of ammonium for amino acid synthesis releases protons (H^+) into the extracellular environment, acidifying the rhizosphere and promoting phosphate dissolution [96], [48]. Using NH_4^+ instead of NO_3^- as a nitrogen source often increases solubilization efficiency [113]. *Bacillus marisflavi* FA7 and *Bacillus subtilis* BPM12 showed maximal P solubilization (272.02 mg L^{-1}) when grown with ammonium salts as nitrogen sources [98, 132]. Multiple studies indicate that proton extrusion may occur through several physiological routes [94, 122].

4.1.4 Indirect mechanism

Indirect P solubilization occurs when microbial turnover via cell lysis under stress releases intracellular P into the soil [23, 54]. Drying-rewetting cycles can greatly reduce microbial biomass P (up to 70%), highlighting environmental control over P availability [66].

4.1.5 Direct oxidation pathway

In Gram-negative bacteria, the oxidation of glucose to gluconic acid via GCD and its subsequent oxidation to 2-ketogluconic acid by gluconate dehydrogenase facilitates chelation of Ca^{2+} and Fe^{2+} phosphates [70]. This pathway is prominent in species such as *Pseudomonas aeruginosa* KR270346 [81] with acidic products diffusing into the extracellular space, lowering pH and releasing P.

4.2 Organic phosphate solubilization

Organic P constitutes 20–30% of total soil phosphorus [74]. PSMs mineralize organic P into plant-available orthophosphate through the enzymatic action of phosphatases, phytases and phosphonatases/lyases, each under genetic regulation.

4.2.1 Non-specific acid phosphatases (NSAPs)

NSAPs, also called phosphomonoesterases, occur as acid or alkaline forms and are produced depending on soil pH [40, 102]. These enzymes hydrolyze phosphoester and phosphoanhydride bonds, releasing P_i from organic matter. Genes including phoA (alkaline phosphatase) and phoD (acid phosphatase) encode these enzymes. The catalytic mechanism of acid phosphatase is illustrated in Fig. 2.

In *Bacillus licheniformis* MTCC 2312, purified alkaline phosphatase application increased phosphorus content in *Zea mays* roots and stems by 2.35 and 1.76 times,

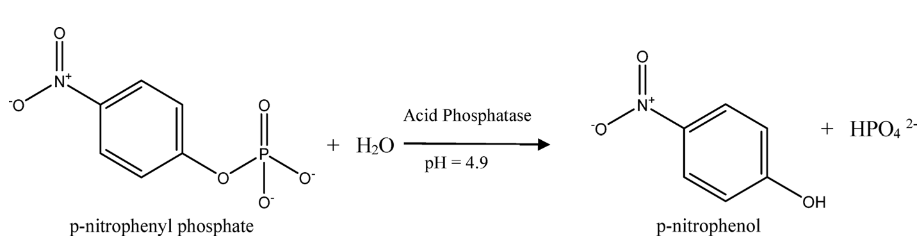


Fig. 2 Catalytic reactions of acid phosphatase [117]

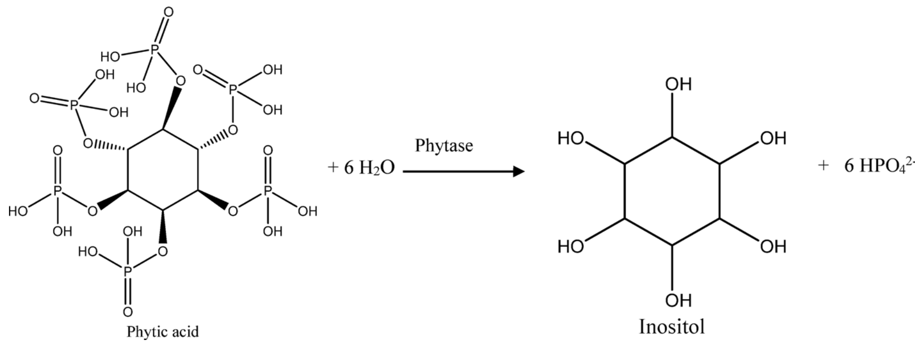


Fig. 3 Catalytic reaction of phytase [58]

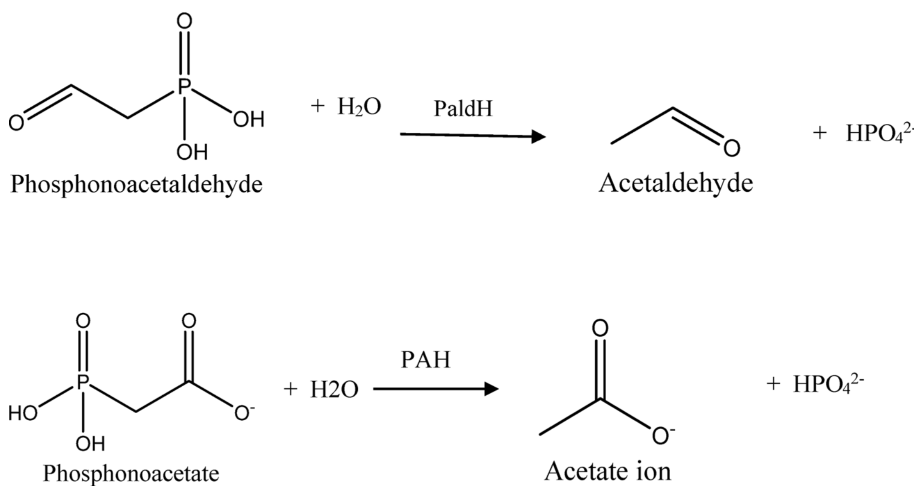


Fig. 4 The catalytic reaction of phosphonatases includes PaldH, which stands for phosphonoacetaldehyde hydrolase and PAH, which refers to phosphonoacetate hydrolase [117]

respectively [120]. Co-inoculation of *Talaromyces helices* L7B with *Rhizophagus irregularis* boosted soil alkaline phosphatase activity from 47.86 EU to 459.38 EU and increased soluble P by 50% [34].

4.2.2 Phytases

Phytates, the main storage form of P in seeds and plant residues, are poorly available to plants. Phytase enzymes, encoded by genes such as appA, hydrolyze phytate to release Pi [114]. The catalytic mechanism of Phytase is illustrated in Fig. 3. Expression of *Aspergillus niger* phyA in *Arabidopsis* improved P nutrition [103].

Aspergillus niger solubilized 835 ppm phosphorus in solid-state fermentation, producing 170 IU phosphatase and 133 IU phytase within 48 h [36]. Phytase-producing *Pseudomonas corrugata* SP77 and *Serratia liquefaciens* LR88 attained solubilization efficiencies up to 714.96 and 306.74 µg mL^{-1}, respectively [15].

4.2.3 Phosphonatases/carbon-phosphorus lyases

These enzymes cleave carbon–phosphorus bonds in organophosphonates, making P bioavailable [26]. The phnX gene encodes phosphonoacetaldehyde hydrolase, a key enzyme in this pathway, catalyzing the hydrolytic cleavage of phosphoacetaldehyde as illustrated in Fig. 4, which also includes phosphonoacetate hydrolase (PAH). Additionally, Fig. 5

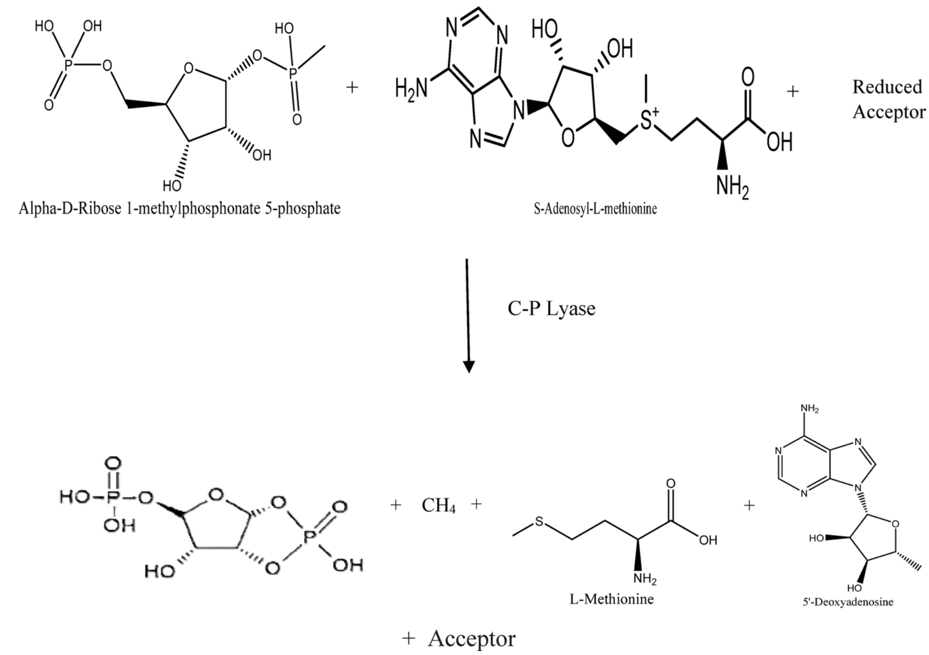


Fig. 5 D-ribose-1-methyl phosphonate-5-phosphate C-P lyase's catalytic process, which forms methane [117]

depicts the catalytic process of D-ribose-1-methyl phosphonate-5-phosphate C-P lyase, which results in methane formation. Although their contribution is smaller due to low substrate availability, activity has been reported in fungi (e.g., *Aspergillus*, *Penicillium*) and bacteria (e.g., *Bacillus*, *Pseudomonas*, *Enterobacter*) [111, 125, 129].

Recent molecular studies have further clarified the genetic regulation underlying key phosphate-solubilizing activities in microorganisms. Genes such as gcd, which encodes glucose dehydrogenase for gluconic acid production, and the pqqABCDEF cluster, crucial for Pyrroloquinoline quinone (PQQ) cofactor biosynthesis (illustrated in Fig. 1), have been identified as central to inorganic phosphate solubilization in various bacteria [37]. Similarly, tricarboxylic acid cycle genes like cit1 are upregulated in fungi such as *Aspergillus* and *Penicillium* during citric acid-mediated dissolution of mineral phosphorus [93]. Moreover, the synthesis of IAA—an auxin that stimulates root growth and supports organic acid release—involves genes including ipdC, highlighting the interconnectedness of microbial P-solubilization with plant development. Phosphatase genes (phoA, phoD) and phytase (appA) have been shown to facilitate organic phosphorus mineralization, while phosphonatase (phnX) contributes to phosphonate breakdown [96]. Critically, these genetic systems are orchestrated via the Pho regulon, notably the PhoR-PhoB two-component system, which modulates gene expression in response to external phosphate availability to optimize uptake and utilization [83], [96]. Additionally, dedicated phosphate transporters—encoded by pit and pstSCAB—enable efficient intracellular phosphate assimilation under conditions of scarcity**.** Notably, enhanced phosphorus incorporation through such mechanisms promotes soil enzymatic activity, improves crop nutritional status and boosts biomass production [60].

5 Applications of phosphate solubilizing microorganisms in crops

Phosphate-solubilizing microorganisms have emerged as vital agents in sustainable agriculture due to their ability to convert insoluble phosphates into bioavailable forms, thereby enhancing nutrient uptake, improving crop productivity and reducing dependency on synthetic fertilizers (Table 4).

5.1 Synergistic effects of microbial consortia

PSM consortia, comprising multiple species with complementary mechanisms, frequently outperform single-strain inoculants in promoting plant growth and phosphorus solubilization. For example, the consortium of Bacillus *megaterium*, *Pseudomonas fluorescens*, and *Aspergillus niger* has demonstrated superior phosphorus solubilization and plant growth enhancement in wheat and maize [64]. Similarly, Qadir et al. [99] reported that a combination of *Bacillus subtilis*, *Pseudomonas putida* and *Enterobacter cloacae* in maize outperformed individual strains by significantly improving plant growth indices, phosphorus availability and soil health through enhanced microbial diversity and organic matter content. The inoculation with the consortium of PGPR-rhizobia-AMF showed an improvement of 130, 200 and 78% in faba bean (*V. faba*) shoot and root dry weight and the number of leaves, respectively. Similarly, shoot and root dry weight and number of leaves of wheat (*T. durum*) were enhanced by 293, 258 and 87%, respectively. In addition, the mineral analyses showed that the inoculation with PGPR-rhizobia-mycorrhizae improved N, P, Ca, K, and Na shoot contents, as well as the contents of sugar and proteins [101]. [69] studied that co-inoculation of *G. intraradices* and *B. subtilis* resulted in 77% greater growth over controls, while single/double inoculations improved microbial biomass, dehydrogenase, urease, phosphatase and protease activities and foliar P and K contents. The dual inoculation of AMF/PGPR and compost significantly enhanced, especially under drought stress, the concentrations of sugar and protein content and antioxidant enzymes (polyphenoloxidase and peroxidase) activities as a defence strategy as compared with controls. Under water stress, it was demonstrated that phosphorus was improved in the inoculated and amended plants alone or in combination in leaves in comparison with controls under severe water stress conditions [7].

Furthermore, Gupta et al. [51] found that integrating *Bacillus subtilis*, *Pseudomonas putida* and *Rhizobium leguminosarum* increased nutrient uptake and biomass in legumes, aided by their ability to occupy diverse ecological niches and promote nutrient cycling. These findings highlight the potential of microbial consortia in integrated nutrient management strategies to reduce fertilizer inputs and mitigate environmental degradation. This idea has been broadened in recent years by focusing on the creation of artificial microbial consortia that combine phosphate solubilization with other advantageous characteristics like stress tolerance, nitrogen fixation and disease suppression. For instance, [46] showed how to create synthetic PSM consortia that are designed to improve stability and functional performance in a variety of soil conditions. This is a promising way to get around the inconsistent results that single-strain inoculants frequently provide. The development of multipurpose biofertilizers that enhance plant health and ecosystem resilience holistically is a growing trend that is consistent with this "multi-trait" approach.

Table 4 Applications of phosphate solubilizing microorganisms and their impacts on crops

Crop	Microorganisms	References	Impact on PSMs Crop
Zea mays	*Bacillus* sp. ACD-9	[77]	Enhanced growth rate by 9%, increased phosphorus absorption by 15%, and reduced acetochlor accumulation by 70%
Zea mays	*Achromobacter*, *Agrobacterium*, *Bacillus*, *Burkholderia*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, *Rhizobia*	[2]	Enhanced growth and phosphorus concentration/absorption
Zea mays, Glycine max	*Bacillus* sp. RZ2MS9 and *Burkholderia ambifaria* RZ2MS16	[13]	Elevated dry weights of roots and shoots versus the control
Zea mays, Glycine max, Arachis hypogaea	*Enterobacter* sp. J49, *Serratia* sp. S119	[84]	Enhanced growth and phosphorus uptake, increased rhizosphere phosphate solubilization, and altered microbial enzyme activities
Pennisetum glaucum	*Bacillus megaterium* UFMG50, *Klebsiella variicola* UFMG51, *Pantoea ananatis* UFMG54, *Microbacterium* sp. UFMG61, *Pseudomonas* sp. UFMG81, *Ochrobactrum pseudogrignonense* CNPMS2088	[118]	Higher phosphorus levels; growth promoted via organic acids, phytohormones
Chenopodium quinoa	*Bacillus licheniformis* QA1, *Enterobacter asburiae* QF11	[86]	Enhanced germination, seedling height/weight; reduced Na^+ uptake under salinity
Glycine max	*Trichoderma* spp.	[20]	Growth improved by 2–41%, and phosphorus uptake efficiency increased up to 141%
Pinus massoniana	*Penicillium guanacastense* JP-NJ2	[100]	Metabolites/suspensions increased shoot length by 60–98%, crown diameter by 28–47%
Camellia oleifera	*Bacillus aryabhattai* JX285, *Pseudomonas auricularis* HN038	[134]	Enhanced growth, photosynthesis, leaf N & P, improved rhizosphere nutrient availability
Solanum lycopersicum	*Arthrobacter* sp., *Bacillus* sp.	[124]	Growth improved 47–115% in P-deficient/saline soils, stronger PGPB effect under salt stress
Solanum lycopersicum, Trigonella foenum-graecum	*Burkholderia gladioli*, *Pseudomonas* sp., *Bacillus subtilis*	[73]	Increased seed germination, plant height, and weight
Triticum aestivum	*Streptomyces alboviridis* P18, *Streptomyces riseorubens* BC3, *Streptomyces griseorubens* BC10, *Nocardiopsis alba* BC11	[21]	Increased root/shoot length (2–24%; 9–24%), root volume (42–72%), root dry weight (47–162%), shoot dry weight (3–66%)
Solanum tuberosum	*Bacillus pumilus*	[136]	Root length up 68%, stem length 79%, fresh plant weight doubled (in vitro)
Phoenix dactylifera	Arbuscular mycorrhizal fungi (*Rhizoglomus irregular*)	[8]	Enhanced growth, leaf water potential, conductivity, and improved physiological parameters
Solanum lycopersicum	*Burkholderia* sp. strain N3	[139, 140]	Promoted growth, increased Cd tolerance
Capsicum annuum, Solanum lycopersicum	*Pantoea vagans*, *Pseudomonas psychrotolerans*, *Bacillus subtilis*, *Bacillus safensis*, *Pantoea agglomerans*	[91]	Promoted growth, reduced pH via gluconic acid
Cucumis melo	*Burkholderia* sp. N3 strain	[139, 140]	Reduced disease incidence of bacterial fruit blotch (– 57.1%)

Table 4 (continued)

Crop	Microorganisms	References	Impact on PSMs Crop
Solanum lycopersicum	AM fungi, *Pseudomonas* sp. 19Fv1T	[19]	Increased sugar and β-carotene concentration in tomato fruits with double inoculation
Fragaria × ananassa	AMF inoculum, *Pseudomonas fluorescens* Pf4, *Pseudomonas* sp. 5Vm1K	[18]	Enhanced yield, fruit taste/quality/vitamin concentration
Solanum lycopersicum	Arbuscular mycorrhizal fungi	[25]	Increased lycopene, total ascorbic acid, alanine, GABA, BCAA, calcium, zinc, ASP, arginine, lysine in cherry tomato fruits
Passiflora edulis	Particulate Organic Matter (POM), *Azospirillum*, PSB, KSB (Potassium Solubilizing Bacteria), VAM (Vesicular Arbuscular Mycorrhiza)	[76]	Maximum leaf dry matter, increased nutrient uptake, improved photosynthetic and metabolic activity
Ocimum basilicum	*Trichoderma*, *Azotobacter*, *Mycorrhiza*	[44]	Increased herb yield, biological and antioxidant activities, and total phenolics/flavonoids

5.2 PSMs in cereal production

Research consistently demonstrates the benefits of PSM inoculation in cereals such as wheat, maize and rice. PSMs enhance phosphorus bioavailability and promote root architecture changes by producing organic acids and enzymes, resulting in improved nutrient uptake and yield. For instance, a combination of *Bacillus megaterium*, *Pseudomonas fluorescens* and *Aspergillus niger* can effectively solubilize phosphorus, leading to enhanced plant growth metrics in crops such as wheat and maize [64]. Another example of the benefits of PSM inoculation in cereal production is a study on sorghum, where inoculation with PSB such as *Pseudomonas putida* strain 168 resulted in substantial improvements in plant height, grain yield and phosphorus uptake under dryland conditions. The study found that seed inoculation with this strain increased nutrient uptake, plant growth and yield metrics, demonstrating a saving of 25% in chemical phosphorus fertilizer application without compromising productivity. In greenhouse trials, inoculated plants had significantly higher shoot growth, ear head weight and P content in both roots and shoots compared to non-inoculated controls and those treated only with chemical fertilizers [105].

5.3 PSMs in legume and pulse production

The synergistic interactions of PSMs with rhizobia stimulate both phosphorus and nitrogen availability in legumes. This dual nutrient enhancement supports improved biomass and yields. Gupta et al. [51] demonstrated that PSM inoculation combined with *Rhizobium leguminosarum* led to higher nutrient absorption and biomass production in legumes, underscoring the complementary role of PSMs in nutrient cycling and biological nitrogen fixation, and Sahu et al. [108] showed that *Bacillus megaterium* and *Pseudomonas putida* consortia increased soil phosphorus availability by 30%, significantly enhancing chickpea growth and yield. Under saline soil conditions, Li et al. [79] observed improved phosphorus uptake and yield in chickpeas using halotolerant PSM strains. Research aimed at developing climate-resilient bioinoculants that are suited for stressful conditions is becoming more and more focused, as evidenced by this trend. However, the complexity of the interactions between legumes, rhizobia and PSM, as well as the unpredictability of the environment, leads to disparities in the outcomes. This suggests that multidisciplinary techniques that combine soil science, plant physiology and microbiology could be used to maximize the efficacy of inoculants.

5.4 PSMs in horticulture and high-value crops

PSMs have shown significant impacts on quality and yield parameters in high-value horticultural crops. In strawberry production, *Bacillus* and *Aspergillus* strains achieved phosphorus fertilizer savings of up to 149 kg P ha^{-1} without compromising yield [50]. Similar benefits were observed in tomato and marigold crops, *Bacillus subtilis* and *Pseudomonas putida* inoculations improved nutrient uptake, vegetative growth, and fruit yield [1, 55]. Additionally, *Pseudomonas luteola* BN0834 increased phosphorus, potassium, and calcium content in apple leaves, enhancing shoot growth [75].

Baloach et al. [11] emphasized the role of PSM inoculation in improving ornamental plant quality and yield, alongside reducing inorganic fertilizer use. In Fenugreek, Sharma et al. [115] reported increased seed production associated with PSM inoculation combined with phosphorus fertilization. Gene-edited *Bacillus* strains produced more organic acid, which improved the bioavailability of phosphorus in tomato crops growing in salt stress, as Altimira et al. [6] showed. Regulatory and ecological factors, however, limit the scalability of such modified strains for commercial horticulture, which is presently being investigated. Furthermore, inconsistent performance across soil types and cultivars suggests that formulations tailored to specific crops and sites are required.

5.5 Dual role of PSMs: biocontrol and growth promotion

Besides nutrient solubilization, some PSMs provide biocontrol benefits by enhancing disease resistance. 139, 140) demonstrated that inoculation of melon with the phosphate-solubilizing bacterium *Burkholderia* sp. N3' reduced bacterial fruit blotch by 57.1%, while also increasing plant growth and nutrient uptake. The study suggested that PSB inoculation induces expression of genes linked to chlorophyll synthesis, metabolism and stress resistance. Mei et al. [91] and Haile et al. [52] corroborated the role of PSMs in stimulating growth and yield in tomato, cucumber and marigold, especially when combined with suitable fertilizer regimes.

6 Soil health improvement and climate change mitigation

PSM consortia contribute to improving soil structure by promoting soil aggregate formation, which enhances aeration, water retention and resilience to environmental stresses such as drought and salinity [135, 138, 141]. By increasing microbial diversity and organic matter, PSMs support sustainable agricultural practices that reduce chemical fertilizer dependency and mitigate climatic impacts.

These microorganisms also facilitate phosphorus recovery from organic wastes like compost and manure, contributing to circular nutrient economies [142]. Moreover, PSMs like *Aspergillus niger* not only improve phosphorus availability but also reduce environmental pollution related to waste disposal. Their integration into nutrient management strategies advances carbon sequestration and decreases greenhouse gas emissions, aiding climate change mitigation efforts [117].

7 Challenges and limitations of phosphate-solubilizing microorganisms

When PSMs undergo transitions from controlled laboratory conditions to complex field environments, they frequently function inconsistently, despite their encouraging promise. This diversity results from a variety of factors that can affect the inoculation strain's ability to survive, colonize and solubilize phosphate, including soil type, environmental circumstances and interactions within local microbial communities. The presence of established native soil microflora frequently leads to competitive exclusion of introduced PSMs, especially in nutrient-rich soils, thereby limiting their effective establishment and functionality [103].

Soil physicochemical properties, including pH, organic matter content, moisture and salinity, additionally modulate PSM activity, sometimes restricting their capacity to solubilize phosphorus and promote plant growth [98]. The interaction between these parameters is complex and not fully understood, emphasizing the need for comprehensive studies to tailor PSM applications to specific agro-ecological contexts. Furthermore, biofertilizer formulations containing PSMs face challenges regarding shelf-life and storage stability, which impact the viability and efficacy of microbial inoculants upon application [12, 42]. Ensuring long-term microbial viability under diverse storage and transport conditions remains critical for commercial success.

From a commercialization perspective, regulatory hurdles and lack of standardised protocols for the production, quality control and application of PSM biofertilizers pose significant barriers to widespread adoption. The variability in national and international regulations can delay product approvals and increase costs, further limiting farmer access to these sustainable technologies.

Lastly, high costs associated with scaling up PSM production and application, coupled with competition from indigenous microbes, constrain the economic viability and reliable field-level performance of PSM-based biofertilizers. To overcome these limitations, it requires integrated approaches combining microbial ecology, formulation technology, agronomic management, and policy frameworks to optimize PSM deployment in sustainable agricultural systems.

8 Recommendations and future perspectives

In order to improve the effectiveness of phosphate solubilizing microorganisms (PSMs) in addressing the phosphorus deficiency in agricultural soil, further studies need to concentrate on three main areas. Identifying and characterizing which PSM strains are advantageous for a particular crop will be essential to maximizing the use of these strains in a range of soil types and climates. Investigating the interactions between PSMs and roots of plants may help to clarify how these bacteria might be utilized to enhance phosphorus uptake and overall plant health. Long-term studies are also necessary to determine how PSM use impacts soil fertility and crop yields in order to establish sustainable agricultural practices. This review discusses the emergence of particular microbial inoculants that improve phosphorus availability, improved crop management strategies that employ PSMs and a better understanding of the ecological roles these microbes play in the nutrient cycle. By addressing these issues, the research can greatly increase sustainable agricultural production and food security in phosphorus-deficient regions.

9 Conclusion

We still don't completely understand how phosphate solubilizing microorganisms interact with plant roots and impact soil health and crop productivity. This requires an in-depth investigation of the metabolic and genetic mechanisms beneath phosphate solubilization in diverse soil types and agricultural systems. Also, Advanced genomic and transcriptomic techniques can help identify novel PSM strains that enhance phosphorus availability. There is also an urgent need for policy frameworks that support PSM-based agricultural solutions. These frameworks need to fund biofertilizer research and training programs focused on sustainable phosphorus management practices.

Author contributions

Rajbala Yadav: Conceptualisation and visualisation, writing original draft, literature on diversity, mechanisms and challenges. Prepared tables and figures. **Ajay Kumar**: Conceptualisation and visualisation, formal analysis, supervision, writing, reviewing and editing. **Meena Sindhu:** Visualisation, resources and grammar editing. **Jagdish Parshad:** Review and editing. **Santosh Ranjan Mohanty, Suruchi Sangwan, Ravi Gautam**: Applications literature survey and editing. **Monika Jangra**: Manuscript review and grammar editing.

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